Non-indigenous Freshwater Plants

Patterns, Processes and Risk Evaluation

Daniel Larson
Faculty of Natural Resources and Agricultural Sciences
Department of Environmental Assessment
Uppsala

Doctoral thesis
Swedish University of Agricultural Sciences
Uppsala 2007

Acta Universitatis Agriculturae Sueciae
2007:15

ISSN 1652-6880
ISBN 91-576-7314-5

Tryck: SLU Service/Repro, Uppsala 2007

Abstract

Larson, D. 2007. *Non-indigenous Freshwater Plants – Patterns, Processes and Risk Evaluation*. Doctoral dissertation.
ISSN 1652-6880, ISBN 91-576-7314-5.

Non-indigenous species (NIS) are species that are moved by man outside their native range. NIS that successfully pass through a number of invasion phases (i.e. introduction, establishment and invasion) are referred to as invasive species. Invasive species potentially cause severe environmental and economic impacts. This thesis highlights the invasion process of non-indigenous aquatic plant species.

Patterns and processes in the establishment phase were assessed with a general focus. The importance of recipient area biodiversity for habitat invasibility was assessed by comparing native species richness in lakes where non-indigenous plant species had become established with non-invaded lakes. It was shown that habitats with established NIS on average had higher native species richness.

Ecological niche modelling was used to test how the continental-scale distributions of non-indigenous freshwater plants in Europe might change during global warming. These models showed that species presently invasive in southern Europe can potentially establish also in northern Europe if the climate gets warmer.

At the invasion phase, focus was more specific to a single species – the floating-leaved freshwater plant *Nymphoides peltata*. Microsatellite analyses of introduced *N. peltata* populations showed that six of seven sampled water systems contained a single genotype. Thus, where the species is introduced, vegetative reproduction constitutes the most important spreading mechanism. Impact of *N. peltata* on submerged species was assessed by using both a modelling approach and using traditional competition experiments. Both approaches showed that submerged plants were negatively affected by low to moderate *N. peltata* densities.

This thesis contributes to a wider understanding of the invasion processes of non-indigenous freshwater plants in general, but of *N. peltata* in particular. Knowledge retrieved from more NIS case studies are needed before general patterns can be assessed.

Keywords: aquatic plant, *Elodea*, impact, invasive species, macrophyte, microsatellite, modelling, non-indigenous species, *Nymphoides peltata*, reproduction

Author's address: Daniel Larson, Department of Environmental Assessment, SLU, Box 7050, SE-750 07, Uppsala, Sweden. *E-mail:* Daniel.Larson@ma.slu.se

Contents

Appendix

Papers I-V

This thesis is based on the following publications, which are referred to by their Roman numerals:

I. Larson, D. & Willén, E. Biodiversity vs. invasibility in Swedish lakes invaded by *Elodea*. In: *Biological invaders in inland waters*. Edited by F. Gherardi. Springer Science and Business Media (Accepted).

II. Larson, D. Ecological niche modelling as a tool for predicting the effects of global warming on the distribution of non-indigenous aquatic plants in Europe (Submitted).

III. Larson, D. 2007. Growth of three submerged plants below different densities of *Nymphoides peltata* (S. G. Gmel.) Kuntze. *Aquatic Botany 86*, 280-284.

IV. Sahlin, U., Larson, D. & Nyberg, C.D. Dose-response impact assessment of non-indigenous aquatic plants and algae – a modelling approach (Manuscript).

V. Larson, D. Reproduction strategies in introduced *Nymphoides peltata* populations revealed by genetic markers *Aquatic Botany* (Accepted).

Introduction

Non-indigenous species (NIS) are species that are moved by man outside their native range. The anthropogenic spread of species can occur across natural barriers, such as seas or deserts. Thus, species are now colonizing environments that they never would have done without the help of man. Some NIS thrive better in their new range than in their native range (Elton, 1958; Keane & Crawley, 2002; Mitchell & Power, 2003). Such NIS can spread widely and are often referred to as invasive species (Richardson *et al.*, 2000). Invasive species often cause severe environmental impacts (Vitousek *et al.*, 1997; Wilcove *et al.*, 1998). They can also directly affect the economy (Pimentel *et al.*, 2000; Pimentel *et al.*, 2001). Introductions of invasive plants have caused loss of endemic species and disruption of entire ecosystems (Mack *et al.*, 2000). The worldwide movement of species across natural barriers, and the consequences on recipient areas, is often referred to as a homogenization of the world's biota (McKinney & Lockwood, 1999; Olden *et al.*, 2004).

It has been hypnotized that the freshwater environment is particularly susceptible to invasions of NIS for a number of reasons. First, aquatic environments are rather homogeneous on a large spatial scale (Santamaría, 2002). This means that many aquatic plants can survive and possibly establish outside their native geographic range (Cook, 1985). It is thus natural that some of the most invasive aquatic plant species have wide distributions (Cook, 1990a). Second, aquatic environments are more difficult to monitor, especially for submerged species, so early detection is seldom possible. Finally, water is an effective vector for propagules, so seeds and vegetative fragments are easily dispersed over long distances.

Many aquatic plant species have been introduced outside their native range (Cook, 1985). Although most do not become invasive, some form dense beds and interfere with human activities such as boating and fishing. Mass developments of non-indigenous plants have the potential to affect native plant species, either by competition or habitat alteration. The effects from non-indigenous aquatic plants are often so severe that control measures are necessary (e.g. Hill & Cilliers, 1999; Moreira *et al.*, 1999; Newman & Dawson, 1999).

Non-indigenous freshwater plants in Sweden

In Sweden, at least 17 plant species have been introduced and since established in freshwater environments (Larson & Willén, 2006). Three of these species *Elodea canadensis* Michx., *Elodea nuttallii* (Planch.) H. St. John and *Nymphoides peltata* (Gmel.) O. Kuntze, are widely distributed within Sweden and are often found in mass developments. The submerged *E. canadensis* was introduced at the end of the 19th century and is now common in most parts of Sweden (Fig. 1a). Another species of the genera Elodea, *E. nuttallii*, was first found at the end of the 20th century and has a more restricted distribution than *E. canadensis* (Fig. 1b). However, since *E. nuttallii* is easily mistaken for *E. canadensis*, its present

distribution might be larger. Furthermore, *E. nuttallii* is probably in an expansion phase and will likely spread to new areas. The introduction pathways of the *Elodea* species are unclear, and both intentional and unintentional introductions have been suggested (Larson & Willén, 2006). For the third widespread NIS in Swedish freshwaters, *N. peltata*, the introduction pathways are better documented and seem to originate from several intended introductions. The first known introduction of *N. peltata* took place at the end of the 19th century, but introductions have also been reported during the last decade. Today, the species is found in 19 different water systems, all in southern Sweden (Fig. 1c).

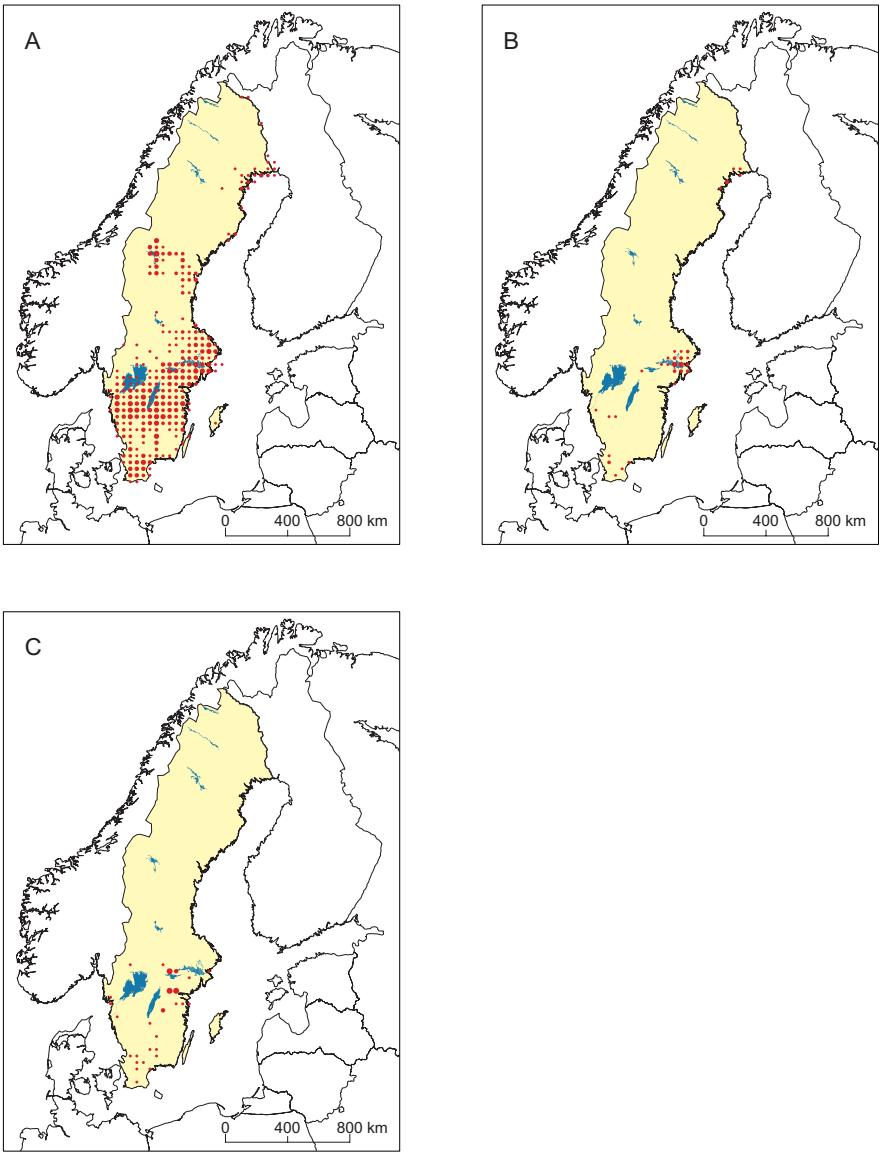

Fig. 1. Swedish distribution of a) *Elodea canadensis*, b) *Elodea nuttallii* and c) *Nymphoides peltata*. Modified from Larson and Willén (2006).

How non-indigenous species become invasive

To become invasive, an NIS must pass a number of barriers, both geographical and ecological. First it must be picked up, transported and released in a recipient area. After arrival, the species must survive and reproduce in order to establish. Once established, the species must increase in number and spread. Hence, the invasion process can be divided into a series of steps and stages (Fig. 2, Heger, 2001; Heger & Trepl, 2003; Williamson, 2006). A general role of thumb is that only about 10% of all species entering any of the given steps will proceed to the next stage (Williamson & Fitter, 1996b). Thus, only a small fraction of those species entering the first step will actually become invasive.

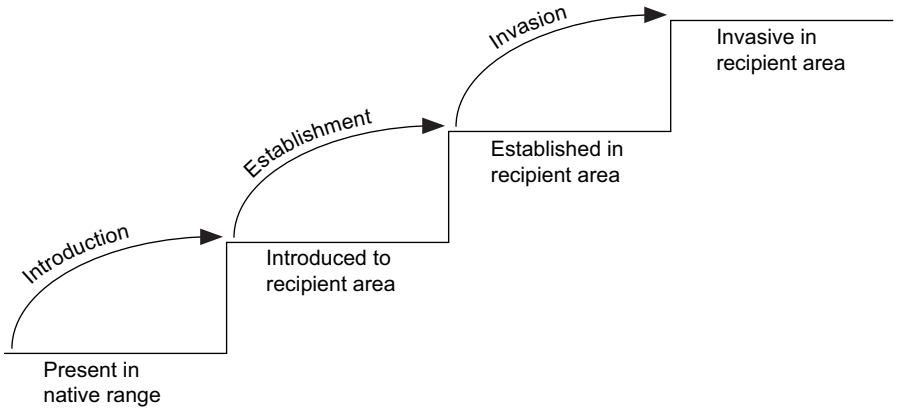

Fig. 2. Steps and stages in biological invasions. Modified from Heger (2001).

Dividing the invasion process into different parts, e.g. a series of steps and stages (Heger, 2001; Heger & Trepl, 2003) or transitions (Kolar & Lodge, 2001) gives us a better understanding of biological invasions. Furthermore, if the invasion process is divided, different approaches can be used to explain the success in different invasion steps.

Introduction phase

To become introduced, a species must be picked up in a donor area, transported to a recipient area, and released into the environment. Species can be introduced either intentionally or unintentionally. Intentional introductions of freshwater plant species include ornamental species (e.g. Cook, 1990a; Maki & Galatowitsch, 2004; Newman & Dawson, 1999), or species used for cultivation (e.g. Hill & Cilliers, 1999). Unintentionally introduced species, on the other hand, are species that are unintentionally picked up, transported and released into a new area. Unintentional introductions of freshwater plants include species that are attached to, or mixed with, intentionally introduced species, and species transported in ballast water.

Introduction success probably differs considerably between species picked up with the intention of introduction and species that are picked up by mistake. Those

that are picked up with intention of introduction are often transported under favourable conditions. Furthermore, the specimens picked up are often the most viable. For unintentionally introduced species, on the other hand, no selection of the most viable specimens is done. Moreover, these species often must survive transport under unfavourable conditions until they are released. However, there is a continuum between what is intentional and what is unintentional in the introduction phase. For instance, a species can be intentionally imported to a region, e.g. for use in aquaria trade (Wallentinus, 2002), but unintentionally released into the environment.

The introduction is the invasion step most influenced by man. Hence, the most important factors controlling which species are to be introduced and to what regions they are introduced are social and economic (Williamson, 2006). However, the driving forces for introduction of species are not static. New driving forces have evolved throughout history, e.g. ancient agriculture millennia ago, human immigrations to newly discovered continents centuries ago and genetically modified organisms the last decades (di Castri, 1990).

Establishment phase

Of those species that are introduced in a new environment, only a fraction will establish viable populations (Williamson & Fitter, 1996b). To become established, the introduced species must survive and reproduce. Survival requires tolerance to the conditions in the new region, determined mainly by climate and water chemistry. Hence, if a species is introduced from a region with similar conditions as the recipient area, the likelihood of survival increases (Baker, 1974). Reproduction often requires that a large number of individuals are introduced, but exceptions are common. For instance, most non-indigenous freshwater plant species are able to reproduce vegetatively. Hence, it is theoretically enough if a single specimen is introduced. Success in survival and reproduction is more likely if the species is introduced intentionally since these species are selected to withstand the conditions in the recipient area and are often introduced in large numbers.

Propagule pressure, i.e. the size of each releasing event and the number of releases, is generally accepted as one of the most important factors for establishment success of introduced species (Lockwood, Cassey & Blackburn, 2005; Lodge, 1993; Richardson & Pyšek, 2006). The more specimens that are introduced, the larger is the likelihood that at least one of them will end up in a suitable spot. Furthermore, a large number of releases increases the likelihood that propagules enter the recipient region during a favourable season of the year.

Invasion phase

Most species that establish viable populations outside their native range do not become invasive. To become invasive, an established species must increase in number and thereafter spread. The spread can either be vector mediated, for instance when plant material is attached to recreational boats (Johnson, Ricciardi & Carlton, 2001; Johnstone, Coffey & Howard-Williams, 1985), or natural, and is

often a complex process (Hastings *et al.*, 2005). Nevertheless, spread from the area of introduction is crucial to risk assessments since the ability to spread will considerably influence the final size of the invaded range. The impact at the site where the NIS first establishes may be negligible, but if transported to more hospitable sites, the species might cause major harm. Species that become invasive can directly affect native species, e.g. through competition. Invasive species can also interact with native species in many indirect ways, e.g. through shared herbivores, parasites and pathogens, and many types of habitat modifications, hence making predictions of impact difficult (Simberloff & Alexander, 1998).

Invasive species are unique in that they thrive in a region in which they have not evolved (Roy, 1990). The lack of evolutionary history between invasive species and species in the recipient area, and that fact that invasive species often have a higher fitness where introduced, has led to the formulation of the enemy release hypothesis. According to this hypothesis, the success of invasive species is due to their escape from specialist enemies that in the native range reduce their abundance (e.g. diseases and herbivores) upon moving to a new range (Elton, 1958; Keane & Crawley, 2002; Mitchell & Power, 2003). Many NIS do escape their natural enemies but new potential enemies, or competitors, might be present in the recipient area. The ecosystem in the recipient area might thus provide biotic resistance. It has been hypothesized that ecosystems with large biological diversity should provide larger biotic resistance (MacArthur, 1972; Tilman, 1999), partly based on observations by Elton (1958) that species poor communities contain more NIS than species-rich communities. However, the opposite is also often observed, i.e. highly invaded species rich areas (e.g. Lonsdale, 1999; Stohlgren, Barnett & Kartesz, 2003; Stohlgren *et al.*, 1999). An alternative hypothesis is that the diversity of a community is a function of its invasibility (Davies *et al.*, 2005). High species richness is then expected as an effect of processes that facilitate establishment. For instance, areas with high habitat heterogeneity or high resource availability can inhabit a large number of species. A large number of species, both native and non-indigenous, will therefore be able to establish in such areas.

Many hypotheses try to explain why only some established NIS become invasive, e.g. the theory of fluctuating resource availability (Davis, Grime & Thompson, 2000). The theory of fluctuating resource availability has also been combined with the enemy release hypothesis into the recourse-enemy release hypothesis (Blumenthal, 2005; Blumenthal, 2006), which states that species adapted to high resource availability that are introduced in high-resource environments will benefit the most from escaping their natural enemies.

It has been also been hypothesized that the success of some NIS is due to evolution after escaping their natural enemies. In the absence of natural herbivore enemies, selection will favour genotypes with higher allocation towards competitive abilities and growth, and lower allocation towards resistance to herbivores (Stastny, Schaffner & Elle, 2005). This has led to the formulation of the evolution of increased competitive ability hypothesis (Blossey & Notzöld, 1995).

Predicting biological invasions

Much effort has been made to predict which species will invade and what habitats will be invaded by NIS (see Richardson & Pyšek, 2006 for a review). However, assessing the risks of NIS is more complex than risk assessments of many other types of environmental threats (Landis, 2004; Simberloff & Alexander, 1998; Stohlgren & Schnase, 2006; Williamson, 1999). For instance, introduced species may evolve or hybridise, and can therefore become more invasive (Rhymer & Simberloff, 1996). Nevertheless, several different approaches have developed in invasion biology. In general, focus has been on either characteristics of the invading species, on those of the invaded environment, or on the relationship between an invading species and an invaded environment (Heger & Trepl, 2003).

Focus on invading species

Since many invasive species have established in many different areas, a straightforward approach is to create lists of species that have proved to be invasive. Such 'black lists' formed one of the earliest NIS risk assessment methods (e.g. Holm *et al.*, 1977). However, since these lists had no ability to predict species not yet invasive, more powerful methods were needed (Mack, 1996). Baker (1974) suggested that many invasive species shared several features and listed a set of characters that would be presented in an 'ideal weed'. Many studies have tested which characters can be used to predict whether a given species will end up in a certain invasion phase or not (Kolar & Lodge, 2001; Mack, 1996; Rejmanek, 2000). Some have compared native species with invasive NIS (e.g. Williamson & Fitter, 1996a), invasive NIS with non-invasive NIS (e.g. Grotkopp, Rejmanek & Rost, 2002; Nyberg & Wallentinus, 2005), or compared NIS from a specific region with species from the same region that have not yet become non-indigenous (e.g. Goodwin, McAllister & Fahrig, 1999; Prinzing *et al.*, 2002). Although a number of characteristics are expected to promote invasion, e.g. having a wide distribution (and thus more likely tolerate a wide range of abiotic conditions) or being of economic importance (and thus more likely to be introduced), the search for particular traits associated with invasiveness has proved difficult (Alpert, Bone & Holzapfel, 2000; Roy, 1990). No invasive species possesses all 'invasive features' and many non-invasive species possesses several of these features (di Castri, 1990).

Focus on recipient areas

Since the number of NIS differs between recipient areas, another predictive approach is to focus on the susceptibility of communities to NIS. The susceptibility of an environment to non-indigenous species is often referred to as the community's invasibility and can be defined as the proportion of introduced propagules that succeed in establishing themselves (Davis, Thompson & Grime, 2005). This proportion is generally very low, and varies in time and from species to species. Although it has been easier to identify characters associated with invasibility than characters of invasive species (Alpert, Bone & Holzapfel, 2000), the methods used to find these characters are sometimes insufficient. When the

invasibility of different regions has been compared, the number of established NIS is often used as a measure of the invasibility. However, the number of established NIS is a function of both number of introduced propagules and the invasibility. Thus, to compare the invasibility of environments, we need to account for the propagule pressure, or at least the number of introduced species that have failed to establish themselves, a task that is often not possible (Lonsdale, 1999).

Nevertheless, a number of characters, both biotic and abiotic, have been suggested to affect the invisibility of communities. For instance, biological diversity has been proposed to act as a barrier for invasions based on the assumption that the higher the number of species present, the more niches are occupied (Elton, 1958; Kennedy *et al.*, 2002; MacArthur, 1972). However, high biological diversity may also indicate high habitat heterogeneity, which in turn increases the likelihood that an introduced species finds a suitable niche for establishment (Davies*, et al.*, 2005; Ortega & Pearson, 2005; Stohlgren, Barnett & Kartesz, 2003). Abiotic factors suggested to affect the invasibility include disturbance and isolation (Elton, 1958; King & Buckney, 2000; Lonsdale, 1999). If the overall probability of finding NIS in different environments is assessed (i.e. not only the invasibility defined as establishment success of introduced species), abiotic factors related to propagule pressure are probably most important (Lockwood, Cassey & Blackburn, 2005; Lonsdale, 1999).

Focus on relationship

Although characteristics of invading species and features of invaded communities partly explain why some species/habitats are more frequently invaders/invaded, the use of these approaches for predictive purposes is low (Roy, 1990; Williamson, 2006). However, the *relation* between characteristics of the invading species *and* features of the invaded ecosystem is often crucial in explaining invasions. For instance, a species can have a broad climatic tolerance that allows it to establish in a large number of regions. Yet, if the species is introduced into a recipient area with climate different from the species tolerance range, establishment is not possible. The most straightforward relational approach is thus to match species' climate tolerance with the climate of potential recipient areas (e.g. Peterson, Papes & Kluza, 2003). Focus on the relationship between NIS and their new environment has also resulted in many promising theories, e.g. the enemy release hypothesis (Keane & Crawley, 2002; Mitchell & Power, 2003), the recourse-enemy release hypothesis (Blumenthal, 2005; Blumenthal, 2006) and the evolution of increased competitive ability hypothesis (Blossey & Notzöld, 1995).

Predicting invasions has proved difficult (Williamson, 2006). Being able to explain which species have already become invasive does not imply that we can predict which species will be the new invaders (Williamson, 1999). Stochastic events do probably play an important role in biological invasions, and which species will become invasive may depend on which species 'catch the right ship' (di Castri, 1990). Rosenzweig (2001) even expressed that considering individual exotic species may be similar to trying to predict which molecules of water will boil off when we heat our coffee. However, considerable progress has also been made during the last 15 years in predicting invasive species (Richardson & Pyšek,

2006) and invasion biology has, and will, contribute to ecological insight (Callaway & Maron, 2006). The most promising risk assessment methods have used different approaches in different invasion steps. For instance, Thuiller *et al.* (2005) made predictions for worldwide introduction and establishment of South African plant species. They used environmental features that increased the propagule pressure (trade routes) in the introduction step, while a relational approach (climate matching) was used in the establishment step.

Objective and structure of this thesis

The overall objective of this thesis was to highlight the invasion process of non-indigenous aquatic plant species. The thesis has two main parts; part one focuses on the establishment phase (Paper I, II) whereas part two focuses on the invasion phase (Paper III, IV, V). Part one has a general focus whereas part two is more specific to a single species – *Nymphoides peltata*. In the following sections, I give a brief overview of the methods to enable a discussion of the obtained results. For a detailed description of the methods, I refer to the original papers.

The major questions addressed were:

- Does biological diversity affect the establishment of non-indigenous freshwater plants at a small spatial scale? (Paper I)
- How will global warming affect the potential distribution of non-indigenous freshwater plants at a continental scale? (Paper II)
- What impact does the non-indigenous freshwater plant species *Nymphoides peltata* have on submerged species? (Paper III, IV)
- How do introduced *Nymphoides peltata* populations reproduce and spread? (Paper V)

Establishment phase: Non-indigenous freshwater plants in general (Paper I, II)

Species that are introduced may or may not establish viable populations. The match between the requirements of the introduced species and the conditions in the recipient area, biotic as well as abiotic, will determine the establishment success. To become established, the introduced species must survive and reproduce. Survival and reproduction are results of different processes acting at different spatial scales.

Lake scale establishment

At the spatial scale of a single habitat, biotic resistance may interfere with establishment. It has been hypnotized that diverse communities are better at repelling invasions (Elton, 1958; Kennedy*, et al.*, 2002; MacArthur, 1972). However, the diversity of a community might also be a function of its invasibility (Davis, Thompson & Grime, 2005). Thus, high species richness can be expected as an effect of processes that facilitate establishment, e.g. habitat heterogeneity. In Paper I**,** a retrospective approach was used to test the importance of recipient area biodiversity on lake-scale establishment of non-indigenous freshwater plants.

Lakes with established populations of either *Elodea canadensis* or *Elodea nuttallii* (hereafter referred to as invaded lakes) were compared with lakes that lacked non-indigenous water plants (hereafter referred to as non-invaded lakes). Data were used from 275 surveyed lakes situated in a small geographical area in central Sweden (Fig. 3). Among the surveyed lakes, 27 were found to have established *Elodea* populations. These invaded lakes were compared with non-invaded lakes regarding native species richness and morphometry. In addition, a subset of the lakes were sampled and compared for water chemistry and proximity to humans.

The number of native plant species was found to be significantly positively related to invasibility. Invaded lakes contained more species than non-invaded lakes (Table 1). Not only was the overall number of species larger in invaded lakes, but so was the number of elodeids, i.e. species of the same guild as the *Elodea* species. However, when assessing biological diversity it is important to consider the spatial scale. Area is positively correlated with species richness, a relation also showed for aquatic plants (Jones, Li & Maberly, 2003; Rørslett, 1991). Spatial scale has also been reported to affect the outcome when assessing the relationship between biodiversity and invasibility (Herben *et al.*, 2004). Therefore, we also compared species richness between sites of similar size. The result showed that even sites with more aquatic plant species were more frequently invaded. This result was obtained both when comparing all sites with and without *Elodea* species, and when comparing only invaded and non-invaded sites within the invaded lakes.

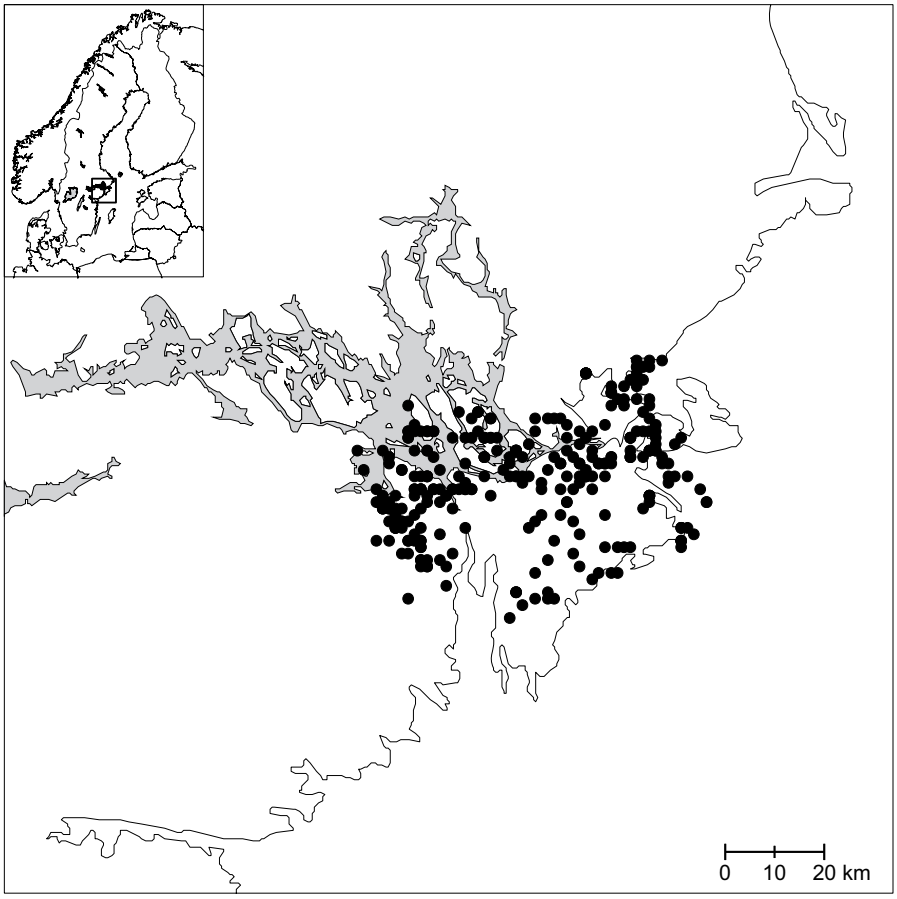

Fig. 3. Lakes used to retrospectively test whether recipient area biodiversity had affected establishment success of non-indigenous *Elodea* species (Paper I).

The pattern that habitats with more aquatic plant species more frequently were invaded by the *Elodea* species needed to be further explored. Our hypothesis was that a shared factor affected both species richness and invasibility, and that the processes were independent of each other. One possible explanation was that the invaded lakes had richer habitat heterogeneity and therefore also more niches to occupy, both for native and non-indigenous species. Therefore, in addition to species richness, lakes were assigned values for their habitat heterogeneity. Both measures of habitat heterogeneity, i.e. lake surface area and shore line irregularity, were larger in the invaded lakes (Table 1), which supports our hypothesis.

Table 1. *Differences in species number and habitat heterogeneity (surface area and shore line irregularity) between invaded and non-invaded lakes. Number of lakes are 275 (27 invaded and 248 non-invaded). Numbers of profiles are 79 and 433 respectively*

	Invaded lakes	*Non-invaded lakes*	
Species number	14	5.5	***
Elodeid number	8.4	2.2	***
Surface area (km^2)	46	0.26	**
Shore line irregularity	3.0	1.6	***

Student's *t*-test: *p<0.05. **p<0.01. ***p<0.001

When searching for relations in nature, it is important to simultaneously consider several mechanisms. Therefore, in addition to our main hypothesis of habitat heterogeneity, consideration was given to other factors affecting the invasion process, i.e. environmental conditions related to the species' demands, propagule pressure and anthropogenic disturbances. To get a comprehensive picture, a subset of the 275 lakes was investigated further. Fifteen non-invaded lakes were compared with 23 invaded lakes for physical and chemical conditions, propagule pressure and anthropogenic disturbances. The result showed that invaded lakes did not differ from non-invaded lakes in most aspects. When reducing the compared variables into two principal components, separation between the invaded and non-invaded lakes appeared on the second axis for principal component analysis (PCA) (Fig. 4a). However, when PCA were performed on chemistry and morphometry variables separately, only morphometry variables successfully separated invaded lakes from non-invaded lakes (Fig. 4b-c).

Invasibility has also been proposed to be affected by the presence of humans due to increased environmental disturbance and transportation of propagules (King & Buckney, 2000). However, in the studied area, the measures of urbanization did not differ for invaded lakes and non-invaded lakes (Fig. 4d). Although propagule pressure was larger for the invaded lakes, interpreted by a higher occurrence of *Elodea* species upstream in invaded lakes (9 of 23) than upstream lakes without *Elodea* species (0 of 15), most invaded lakes also lacked invaded upstream lakes. Such a coincidence suggests invasions from other pathways and that both types of lakes may be under similar propagule pressure.

The best indicator of *Elodea* establishment was the diversity of other aquatic plant species, which in turn is an indicator of habitat heterogeneity. We found no evidence for any causal relationship between invasibility and species richness. However, we suggest that the same underlying factors affect the richness of non-indigenous and native species. One such factor is probably the habitat heterogeneity.

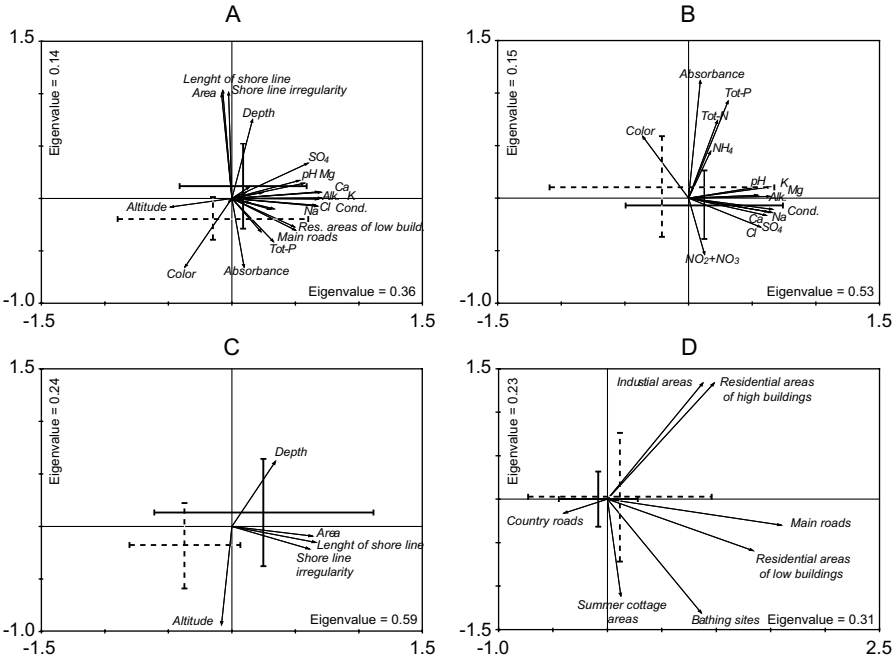

Fig. 4. Principal component analyses of water chemistry, morphometry and urbanization in lakes with and without *Elodea* species. Mean and SD of invaded lakes (solid crosses, n = 23) and non-invaded lakes (dashed crosses, n = 15).

a) Water chemistry, morphometry and urbanization (p-value of second ordination axis = 0.003)

b) Water chemistry variables

c) Morphometry variables (p-value of first ordination axis = 0.008 and second ordination axis = 0.044)

d) Urbanization variables

Only p-values below 0.05 are specified

Continental scale establishment

At larger spatial scales, climate is a major factor controlling the distribution of plants (Huntley, 1991; Skov & Svenning, 2004). Because of global warming, many NIS are expected to be able to establish in regions not previously possible. One method to assess the effects of global warming on the distribution of specific NIS is ecological niche modelling. Ecological niche models are based on species distribution data and climate data, where the simplest forms build a climate envelope based on the most extreme conditions, or percentiles thereof, from the species' known range. Ecological niche modelling constitutes one of few methods for assessing the effects of global warming on the potential distribution of NIS (Baker *et al.*, 2000; Hannah, Midgley & Millar, 2002; Pearson & Dawson, 2003). Although it is not possible to verify these models on climate scenarios that have not yet occurred, spatial uncertainty can be used as a proxy of the temporal

uncertainty. In Paper II, ecological niche modelling was used to test how the continental-scale distribution of non-indigenous water plants in Europe might change during global warming.

Habitat suitability was modelled for 13 non-indigenous freshwater plant species using a maximum entropy approach (Phillips, Anderson & Schapire, 2006). Suitability was modelled for current climatic conditions and for one future climatic scenario (a $2\times CO_2$ climate CCM3 model for the year 2100). Uncertainty was assessed by testing the degree of transferability for models based on species' European distribution to a dataset outside Europe. Thus, for each species, two types of models were created; one based on the species distribution outside Europe and one based on the species distribution within Europe. Models based on the distribution outside Europe were only used to assess the uncertainty when transferring the European model to a different set of environmental data (Fig. 5a), whereas models based on distribution within Europe additionally were projected onto a future climate scenario and used to assess the climate induced distribution shifts (Fig. 5b). A transferability uncertainty interval (TUI) was calculated from the ability of European models to predict modelled non-European distributions. The TUI was used to determine whether future models deviated from current models more than expected as a result of misclassification.

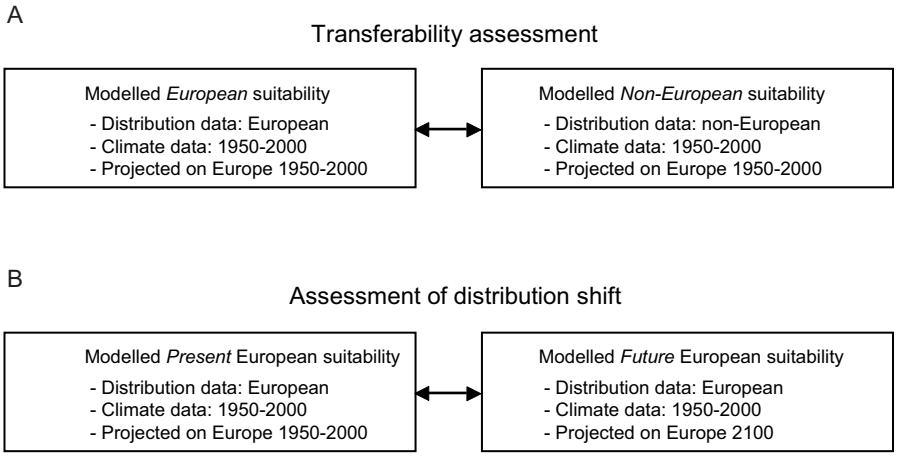

Fig. 5. Modelling approach showing processes and data used for a) assessing the transferability and b) assessing the distribution shifts (Paper II).

Ecological niche models showed that most species lost more suitable habitats than they gained although uncertainties in modelled niches were large (Fig. 6). Eight species lost larger suitable areas than expected due to misclassification. Two of these species, *Alisma gramineum* Lej. and *Elodea canadensis*, also gained larger areas than expected.

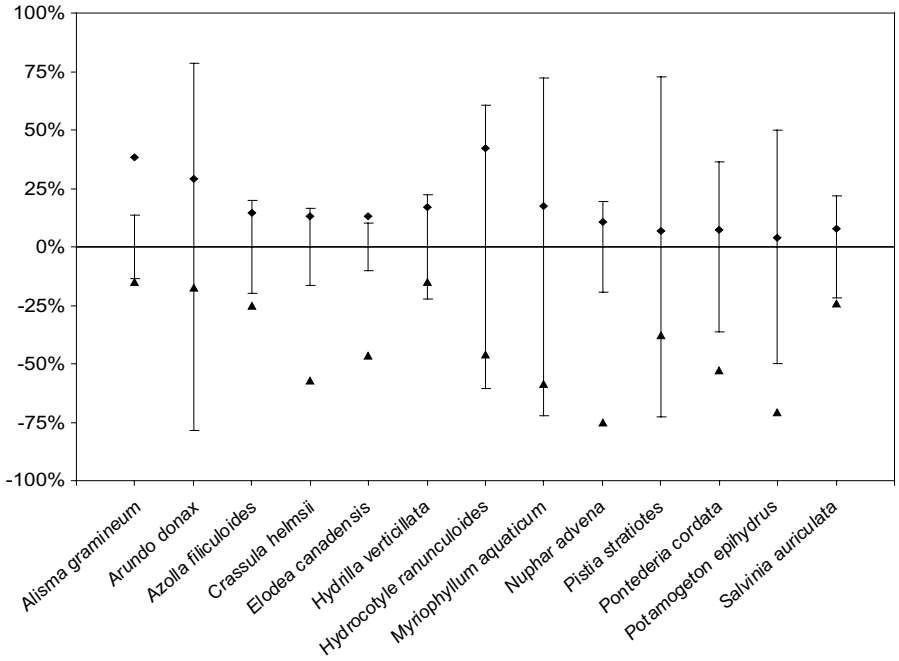

Fig. 6. Gained and lost potential distribution areas for 13 non-indigenous aquatic plant species in Europe as a result of global warming. Error bars indicate transferability uncertainty. Values and uncertainties are percentage of current potential distributions.

♦ gained suitable areas in the future climate scenario

▲ lost suitable areas in the future climate scenario

Although our results indicated an overall decrease in suitable areas for 10 of 13 species on a European scale, this was not seen on a smaller scale. Whereas some parts of Europe lost potential suitable areas, others were predicted to gain potential suitable areas. The general pattern among the assessed species was that the southern parts of Europe will lose suitable areas, whereas suitable areas will be gained in the north (Fig. 7). However, it is important to stress that the maps in Fig. 7 represent the *potential* distribution of the species, and other factors such as dispersal and biotic interactions will further influence their range (Davis *et al.*, 1998; Guisan & Thuiller, 2005; Pearson & Dawson, 2003). Furthermore, to create binary maps of potential distributions from modelled suitability, a threshold value must be applied. Cells with suitability values above the threshold value are included in the potential distribution. The exact sizes and locations of the modelled distributions are therefore not expected to be accurate. For instance, the recorded distribution of *E. canadensis* in England is much larger than the potential distribution modelled for the current climate. Nevertheless, the general pattern observed, with a distribution shift towards the north for many species, is independent of threshold value.

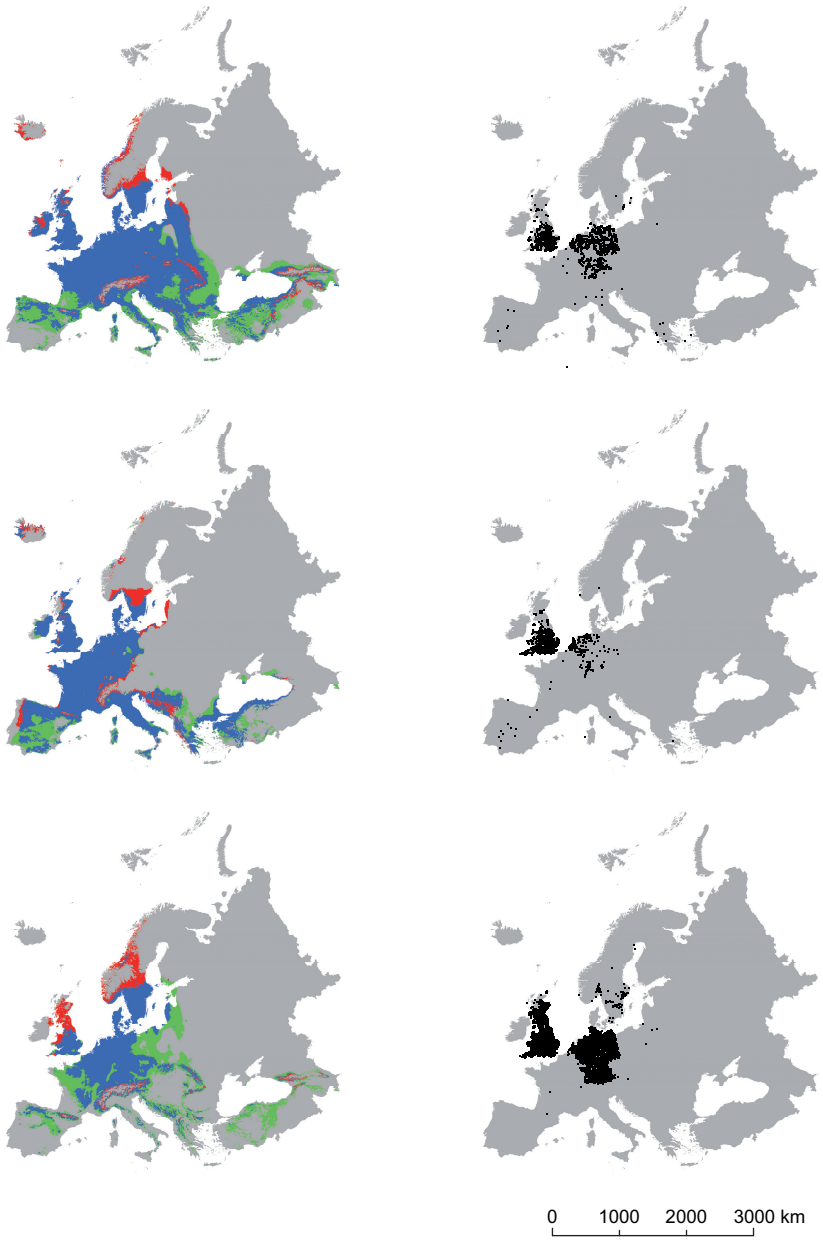

Fig. 7. Potential (left) and recorded distribution (right) for *Alisma gramineum* (top), *Azolla filiculoides* (middle) and *Elodea canadensis* (bottom) based on a single threshold value. Green areas are predicted as suitable at current climate only, blue areas are predicted as suitable at current and future climate, and red areas are predicted as suitable at future climate only.

Since the potential distribution for most species might move northward as a result of global warming, we need to consider the possibility that NIS that today are only established in southern parts of Europe might spread to the northern parts.

In areas where established NIS can be expected to decrease due to reduced suitability, species not yet established in Europe might establish if introduced. Furthermore, already established but not yet invasive species that are in the margin of their distribution today might gain fitness from global warming and increase in abundance, and possibly become invasive. Simultaneously, since native species are also affected by an altered climate, changes in the biotic resistance of communities can be expected.

Invasion phase: *Nymphoides peltata* in particular (Paper III, IV, V)

To become invasive, established species must increase in number and spread. Species that do become invasive can cause major harm to recipient ecosystems, either by directly affecting native species (e.g. competition) or in less predictable indirect ways such as habitat modification (Simberloff & Alexander, 1998). Since the size of the invaded range is one key factor that determine the impact of an NIS, spread from the area of introduction is crucial to risk assessments (Parker *et al.*, 1999). Furthermore, impact at the site where the NIS first establishes may be negligible, but if transported to more hospitable sites, the species might cause major harm.

Studied species – *Nymphoides peltata*

Nymphoides peltata is a floating-leaved freshwater plant indigenous to Central Europe and Asia Minor that has been introduced outside its native range (Cook, 1985). It can reproduce both sexually and vegetatively, and seeds can be produced by different forms of pollination. The simplest form is self-pollination, which can take place either within a single flower or between different flowers on the same genetic individual. On the other hand, cross-pollination can either take place within or between morphs as *N. peltata* is a distylous plant. In dimorphic populations, production of more than 3000 seeds per m^2 has been observed (van der Velde & van der Heijden, 1981). However, fruits originating from self- or within-morph pollinated flowers have fewer seeds than fruits from cross-pollination between morphs due to partial self-incompatibility (Ornduff, 1966; van der Velde & van der Heijden, 1981). Although seeds from self- or within-morph pollinated flowers easily germinate, seedling viability is low and few seedlings survive beyond the cotyledonare stage (Ornduff, 1966). Yet, given the large number of seeds produced, only a fraction needs to germinate at favourable locations to rapidly colonize a water body.

Established *N. peltata* plants expand locally with runners (Fig. 8, see van der Velde, Giesen & van der Heijden, 1979 for a more detailed description of the species). These runners allow a single plant to colonize large areas within a few years (Brock *et al.*, 1983). If the runners have developed roots that are not yet attached to the sediment and the runners break, vegetative fragments will be released and eventually transported to favourable sites where they can establish. In addition to vegetative reproduction from broken runners, secondary propagation occurs by plantlet development at the flowering stems (Ornduff, 1966; van der Velde & van der Heijden, 1981). The ability to reproduce vegetatively is evidently an important part of the reproduction strategy in *N. peltata* since monomorphic and possibly genetically uniform populations occur (e.g. Uesugi *et al.*, 2004; Wang *et al.*, 2005). In introduced populations, particularly, where it is most likely that only a single morph or even a single clone has been introduced, vegetative reproduction may be the only mode of dispersal.

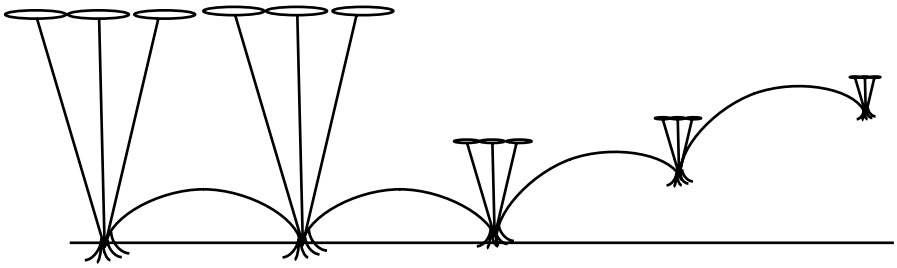

Fig. 8. Schematic description on how *Nymphoides peltata* expand locally with runners.

N. peltata was first introduced deliberately in Sweden in the late 19th century and is now considered as the non-indigenous plant species posing the largest threat to biological diversity and economic value of Swedish freshwaters (Larson & Willén, 2006), but the actual impact has never been quantified. In several of the more than 30 lakes and watercourses distributed over 19 larger water systems where it has been found, *N. peltata* forms dense stands over such large areas that control measures are necessary. The invasion is probably due to several introductions but knowledge of many of these is sparse. Even where the time of introduction is known, source populations and the number of propagules are often unknown.

Impact of *Nymphoides peltata*

Few studies have assessed the impact of invasive species on the aquatic plant community, but those existing illustrate severe ecological effects. For instance, Boylen, Eichler & Madsen (1999) showed that the invasion of Eurasian water milfoil *Myriophyllum spicatum* L. in the northwest bay of Lake George, New York, reduced the number of aquatic plants from 20 to 7 species in only 11 years as a consequence of the rapid, dense growth of the non-indigenous species. Although it is interesting to explain the effects of a certain invasion event, measuring the impact in nature is complicated (Parker*, et al.*, 1999). For example, the experimental design needs to separate the effect of the invasive species from other processes such as global warming and eutrophication, and to consider the complexity of synergistic interactions between invasive species and other stressors. Monitoring the invasive event also needs to be started before the actual invasion takes place, which requires that the invaded site is already included in a monitoring programme. Furthermore, control sites need to monitored, both before and after the event to separate the effect of the invasion from other effects (i.e. BACI design, see Stewart-Oaten, Murdoch & Parker, 1986). Moreover ethical, even juridical concerns should be considered if we suspect a species to be invasive. In those cases we may be obliged to immediately start eradication or control measures instead of monitoring. Even if we succeed in measuring the impact of an invasion event, we can seldom use the outcome to predict the effects in other cases. To make predictions we need to be aware of the causal relationships between the invasion process and the impact on the different parts of a certain ecosystem.

Impact of Nymphoides peltata on three submerged plant species

To assess the impact from *N. peltata* on other plant species, the one-sided competition between *N. peltata* and three submerged species were investigated in an experimental study (Paper III). The aim was to quantify the shading effect from *N. peltata* on the growth of the species *Ceratophyllum demersum* L., *Elodea canadensis* and *Ranunculus circinatus* Sibth. It was hypothesized that growth rates of all three species would decrease with increasing *N. peltata* cover.

Seedlings of *N. peltata* and the three submerged species were collected in nature and transplanted into a greenhouse pond. The pond were divided into four compartments, separated only by a plastic net, thus eliminating differences of other factors such as allelopathy and nutrient levels between treatments. The degree of *N. peltata* cover within each compartment was adjusted by mechanically removing *N. peltata* stems to surface densities of approximately 0, 33, 66 and 100% (Fig. 9).

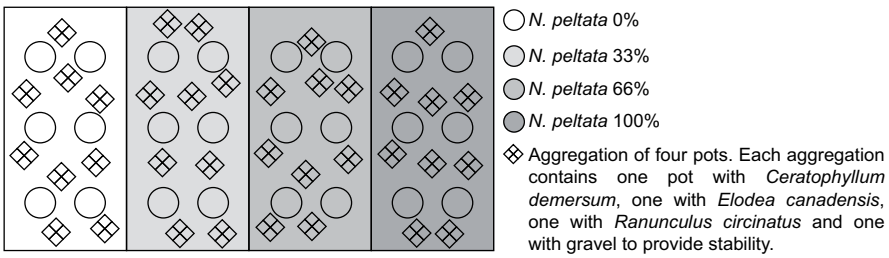

Fig. 9. Experimental setup of competition study (Paper III).

After 7, 14 and 21 days of growth, three plants of each submerged species were harvested from each compartment, measured for length and weighed. The measurements of dry weight and length were used to calculate the species relative growth rate (RGR) under different *N. peltata* densities. RGR were plotted against the percentage of area covered and, where possible, a regression line based on the Michaelis-Menten equation was fitted:

$$P(PAR) = const + P_{\max}\frac{PAR}{K_m + PAR}$$

P is the photosynthesis; const the constant; P_{max} the maximum possible photosynthesis; K_m the light intensity where P is one-half of P_{max}; PAR is the irradiance (photosynthetically active radiation)

All three submerged species responded with reduced growth rates when *N. peltata* was present (Fig. 10). The RGR of *C. demersum* and *E. canadensis* decreased already at moderate *N. peltata* densities, whereas the weight based growth rates of *R. circinatus* required high densities to be affected. Not only were the three species affected by the presence of the floating-leaved species, they also differed in their response to different *N. peltata* densities as revealed by the species × *N. peltata* density interaction (Table 2). Since interspecific competition may be the mechanism most important for the structure of the submerged plant

community (McCreary, 1991), this result implies that different parts of the submerged plant community are affected to a different extent.

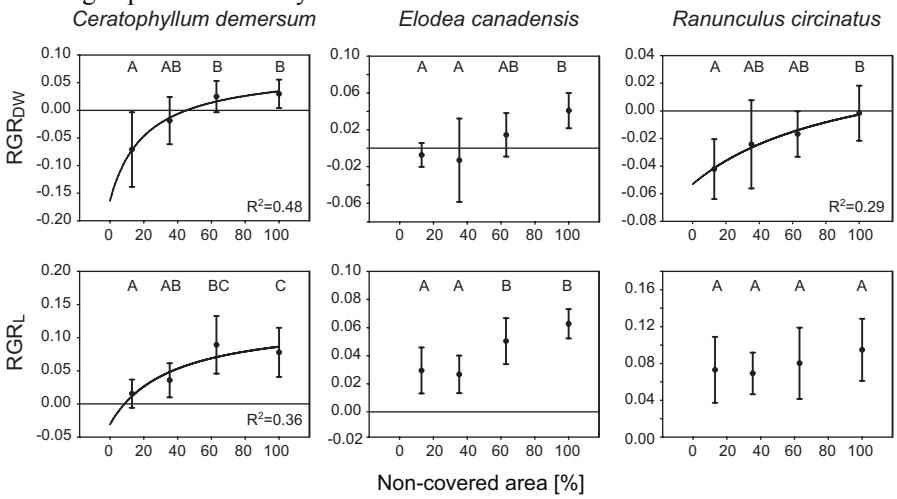

Fig. 10. Response to different *Nymphoides peltata* densities for *Ceratophyllum demersum*, *Elodea canadensis* and *Ranunculus circinatus*. Means and standard deviation of relative growth rate (day^{-1}) based on dry weight and length. Mean values with different letters are significantly different ($p < 0.05$, Tukey's test). Regression lines are based on the Michaelis-Menten equation.

Since all submerged species responded with negative weight growth already at moderate *N. peltata* densities, one-sided competition from the floating-leaved macrophytes profoundly affects the submerged plant community. Hence, if *N. peltata* invades areas where submerged species grow without floating-leaved species, considerable alterations in the structure of the submerged plant community are plausible.

Table 2. *Two-way ANOVA of RGR based on dry weight and length of Ceratophyllum demersum (n = 29), Elodea canadensis (n = 35) and Ranunculus circinatus (n = 35) growing under different Nymphoides peltata densities*

Source of variation	DF	RGR_{DW}			RGR_L		
		MS	F		MS	F	
Species	2	0.008	8.21	***	0.012	15.40	***
N. peltata density	3	0.018	18.81	***	0.010	11.91	***
Species × *N. peltata* density	6	0.002	2.58	*	0.002	1.93	ns

Impact of Nymphoides peltata on a threatened submerged plant species

Although controlled competition experiments can estimate the effects from an NIS on native species, results from such studies cannot be directly transferred to large-scale natural conditions. For instance, introduced species can also interact with native species in many indirect ways, e.g. through shared herbivores and many types of habitat modifications (Simberloff & Alexander, 1998). To assess the overall impact of NIS, these indirect effects should be considered. In Paper IV, a modelling approach that accounted for both direct and indirect effects was used to

evaluate the impact of *N. peltata* on an already threatened submerged plant species, *Alisma wahlenbergii* (Holmb.) Juz.

A model was constructed that describes how the non-indigenous *N. peltata* affects physical characteristics of the aquatic environment, and how these physical characteristics in turn affect the threatened species. Two pairs of non-indigenous/indigenous species were used as model organisms: the freshwater plant species, *N. peltata* and *A. wahlenbergii*, and the marine macrophytes, *Gracilaria vermiculophylla* (Ohmi) Papenfuss and *Zostera marina* L. First, one conceptual model was created for each of the two species pairs. Thereafter, the two models were condensed into a single conceptual model (Fig. 11). The common conceptual model was then transformed into a quantitative model. Thus, all causal relationships were given functional expressions, ranging from mathematical functions from established models, to simple functions expressing directions or categorical relations. Variability was included as stochasticity in causal relationships and as daily variation in parameters.

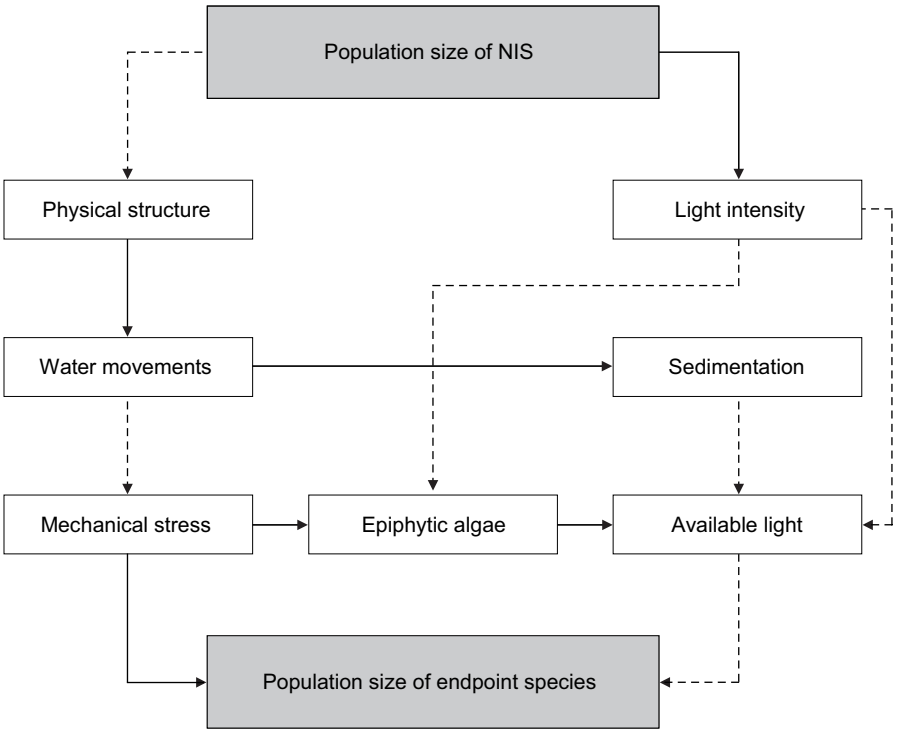

Fig. 11. Conceptual model showing selected variables and links that create a path from the NIS *Nymphoides peltata* to the endpoint species *Alisma wahlenbergii* (Paper IV). Solid lines indicate negative causal links and dashed lines positive causal links.

The quantitative model was run as a one-dimensional Monte Carlo simulation in Palisade @RISK platform in Microsoft Excel. The model was run with different parameterizations that caused different densities of the NIS. Thus, dose-response relationships between NIS biomass and change in biomass of the indigenous

(endpoint) species were obtained, hereafter referred to as impact curves. Prior to model runs, different impact classes were defined based on current status of the endpoint species. In the *N. peltata – A. wahlenbergii* case, impact was stated to be negative for all losses in biomass of the endpoint species exceeding 5%.

The impact curve indicated a rapidly increasing probability of a negative effect with the abundance of *N. peltata* (Fig. 12). At low *N. peltata* abundances, the NIS most probably did not affect the endpoint species at all. Positive effects were possible at all *N. peltata* abundances although the probability for positive effects was low.

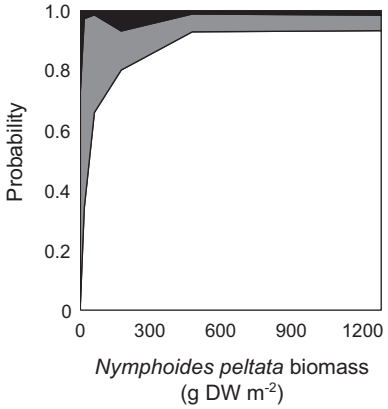

Fig. 12. Impact curve showing the effect of *Nymphoides peltata* on *Alisma wahlenbergii.* Areas are probability of a negative effect (white), no effect (grey) and positive effect (black).

Although the probability of a negative impact was large, the uncertainty of the impact curve was considerable. For some *N. peltata* densities, the probability for a negative impact even ranged from 0 to 1 (Fig. 13). However, as the abundance of the NIS increased the uncertainty in the predictions of a negative impact decreased. This is in line with what is to be expected, i.e. that the higher dose of the stressor, the more robust is the effect on the endpoint.

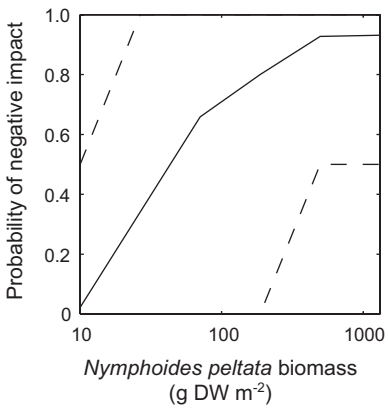

Fig. 13. Impact curve with uncertainty. Mean probability (solid line) and uncertainty (dashed line) for negative impact on *Alisma wahlenbergii* at different *Nymphoides peltata* abundances.

The impact curve describes how the endpoint species reacts to the presence of the NIS, and has much in common with the so-called dose-response curve used in toxicity testing. A major difference is that the stressor (i.e. the NIS) and the endpoint interact, and it is not possible to directly control the level of the stressor. The impact curve can, in accordance with the dose-response curve, be used to find a highest acceptable abundance of the biomass of the NIS in a region, by determining an acceptable threshold for the probability of a negative impact. For instance, if the accepted risk is 50%, the highest acceptable biomass of *N. peltata* is 50 g DW m^{-2} (dry weight) if we disregard the uncertainty (Fig. 13). However, if we choose to account for the included uncertainty, the highest acceptable *N. peltata* biomass is 10 g DW m^{-2}.

The abundance of *N. peltata*, where introduced, often reaches surface covers of 50% or more. The biomasses that pose a 50% risk for negative effects on the endpoint species (dry weights of 50 g m^{-2} if uncertainty is not considered, or 10 g m^{-2} when uncertainty is considered), correspond to leaf areas of 0.36±0.14 m^2 m^{-2} and 0.071±0.028 m^2 m^{-2} (van der Velde, Giesen & van der Heijden, 1979). However, the actual surface covers associated with the highest acceptable biomasses are probably only one half of the leaf surface area since leaves often overlap. A 50% risk for negative effects on *A. wahlenbergii* is thus reached already at surface covers of less than 20% if uncertainty is not considered, or less than 5% when uncertainty is considered. Given the usual high abundances of *N. peltata* where introduced, we can thus expect the NIS to cause negative effects if it establishes in areas where *A. wahlenbergii* grows.

Spread of *Nymphoides peltata*

The reproduction and spread of an NIS will affect the species' population size, and thus its overall impact. Information on the reproduction is thus crucial in risk assessments of NIS. *N. peltata* can reproduce both sexually and vegetatively, and seeds can be produced by different forms of pollination. To design a weed control or eradication programme, knowledge is needed of the species' reproduction strategy and dispersal mechanisms. Like many other clonal aquatic plants, the relative importance of different reproduction strategies in *N. peltata* is poorly understood (Wang, *et al.*, 2005). Many clonal plants change their reproduction behaviour when introduced in small numbers, which makes predictions of reproduction at introduced sites difficult (Barrett, 1992). Therefore, the modes of spread in introduced *N. peltata* populations were investigated using molecular markers (Paper V).

Microsatellites were used to determine the past spread of Swedish *N. peltata* populations. This technique was chosen because of its high resolution, the low risk of contamination and because microsatellites are already developed for *N. peltata* (Uesugi *et al.*, 2005). Of the 19 water systems in Sweden where *N. peltata* has been found, 7 were sampled. In each system, 2-12 colonies were sampled, depending on the total number of colonies. From each colony, three or five fresh leaf samples were taken in a way that maximized the likelihood of sampling different individuals.

DNA was extracted from leafs in duplicates. Prior to DNA extraction, leaf segments were homogenized and centrifuged. Extracted DNA solutions were amplified with seven of the eight primer pairs designed by Uesugi *et al.* (2005) using Polymerase Chain Reaction (PCR). The PCR products were electrophoresed along with a size standard, and results from the electrophoresis were interpreted as genotypes.

The microsatellite analyses showed that all water systems except the Lake Glan system contained a single genotype (Fig. 14). This result suggests that reproduction in these populations is entirely vegetative. On the other hand, in the Lake Glan system, eight genotypes were found among the 36 analysed samples. However, a large number of samples with the A-genotype in Lake Glan (n=18) suggests that even in this population, vegetative reproduction constitutes an important part of the total reproduction.

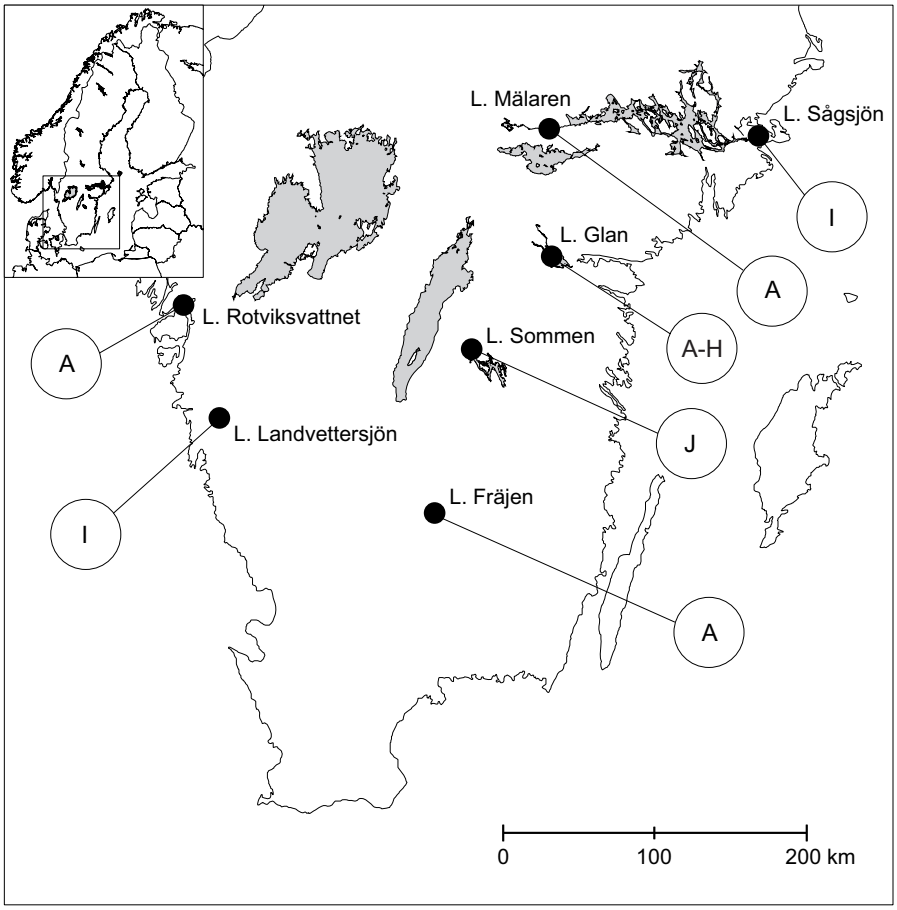

Fig. 14. Genotypes of sampled *Nymphoides peltata* leaves based on microsatellite analyses in seven Swedish water systems.

The ability to reproduce asexually is clearly advantageous for *N. peltata* when introduced to distant areas. Introductions are non-frequent events involving few

propagules of which only a fraction will establish (Williamson & Fitter, 1996b). Hence, with small population sizes and low species densities, Allee effects due to mate shortage can considerably affect the establishment of sexually reproducing species (McCarthy, 1997; Taylor & Hastings, 2005). With a small number of initial founders, sexual reproduction can also lead to loss of alleles due to inbreeding (Barrett & Husband, 1989). Vegetative reproduction eliminates the need for a partner. Furthermore, it can freeze a genotype in a sexual population, and thus preserve a high level of heterozygosity (Vrijenhoek, 1990).

However, vegetative reproduction has some obvious drawbacks. Vegetative fragments are not as easily dispersed to new areas as seeds that are adapted to bird transportation (Cook, 1990b). Further, without seed production, no persistent seed bank is formed and hence, stochastic events may cause the population extinction (Wang*, et al.*, 2005). Where seed reproduction occurs, persistent seed banks are formed, which can tolerate extreme conditions such as desiccation, frost and hypoxia (Guppy, 1897; Smits, van Avesaath & van der Velde, 1990). The absence of persistent seed banks in introduced *N. peltata* populations has the effect that stochastic events that would otherwise only cause temporal extinction instead may lead to permanent extinction. Moreover, the long-time persistence of vegetative reproducing populations is endangered due to lack of evolutionary potential, which is needed to respond to environmental changes (Ornduff, 1966).

Conclusions and future perspectives

Invasions of non-indigenous freshwater plants are serious. Previous events, such as the invasion of the water hyacinth *Eichhornia crassipes* (Mart.) Solms-Laub. in Lake Victoria (Albright, Moorhouse & McNabb, 2004) should serve as a warning sign before new introductions take place. However, it has proved difficult to predict which species will invade and what habitats will be invaded by NIS. This thesis showed that information on characteristics of recipient habitats, such as their species richness, is often insufficient to predict which habitats will be invaded (Paper I).

Freshwater plant species that do become invasive can cause major harm to recipient ecosystems. This thesis showed that *N. peltata* affects the growth rate of several submerged plant species; in Paper III, all submerged species responded with negative weight growth at moderate *N. peltata* densities, and the impact curve of Paper IV showed high probabilities for negative impact on *A. wahlenbergii* already at low *N. peltata* densities. Thus, *N. peltata* have the potential to cause alterations in the submerged plant community. Such alterations are likely to affect several other levels in the food web (Diehl & Kornijów, 1998; Wetzel & Søndergaard, 1998).

Vegetative reproduction seems to be the most important reproduction strategy in introduced *N. peltata* populations. The ability to reproduce vegetatively eliminates the need for a partner. Thus, establishment is possible even if only a single specimen is introduced. Furthermore, the ability to reproduce vegetatively is advantageous even when sufficient numbers of propagules to allow sexual reproduction are introduced. Vegetative reproduction can lead to a more rapid spread than seed reproduction: vegetative fragments can develop into new plants that disperse new fragments several times each growing season, whereas seeds need to overcome dormancy before they can germinate.

To avoid impact on the submerged plant community in already invaded lakes, as well as to restore recreation values, established populations of *N. peltata* need to be treated and further spread needs to be stopped. Aquatic weeds can be managed in several ways, e.g., harvesting, water-level fluctuations, alterations in light and nutrients, herbicides and biocontrol (see Nichols, 1991 for an extensive review). The absence of seed reproduction in most introduced *N. peltata* populations will facilitate eradication measures and the absence of persistent seed banks will reduce the risk of re-establishment. If eradication is not possible, the weed can be maintained at an acceptable level through control measures.

At present, repeated cutting is used as control measure at several *N. peltata* invaded water systems. This method gives only short-time effects, and where mechanical control has been used for several years, the population density has not been reduced. The main problem of clipping is that cut-off fragments, if not collected, are transported by water currents to new areas where they may establish new colonies. Hence, this method can actually increase the rate of spread. Given the importance of vegetative reproduction shown in Paper V and the many fragments released at each cutting occasion, it is most likely that cutting

constitutes an important factor of the recent spread. At the same time, if these populations are left untreated, the spreading will continue either by establishment of rooted stems that have broken due to natural causes or by secondary propagation. Therefore, a more comprehensive control or eradication programme should be adopted.

In Sweden, relatively few non-indigenous freshwater plant species have succeeded in all invasion phases. With the predicted global warming, new species will have the potential to establish if introduced, and possibly become invasive (Paper II). Therefore, we need to consider that NIS presently invasive in central Europe might spread to Sweden and become invasive. However, aquatic plant species might have a larger tolerance than revealed by ecological niche models. Thus, we should be cautious and consider all NIS as potential invaders until the opposite is proved.

Svensk sammanfattning

Spridningen av främmande arter utgör ett påtagligt hot mot den biologiska mångfalden och medför i många fall svårlösliga praktiska problem. När arter introduceras i områden där de aldrig tidigare funnits finns risken att de etablerar sig och tillväxer explosionsartat. Denna avhandling belyser mönster, processer och riskbedömning av främmande växter i sjöar och vattendrag och är baserad på fem studier.

I den första studien undersöktes betydelsen av sjöars artrikedom för etablering av främmande vattenväxter. Studier av andra typer av främmande arter har visat på färre främmande arter i artrika miljöer än i artfattiga miljöer. Den mest vedertagna förklaringen har länge varit att artrikedomen utgör ett slags skydd mot nyetableringar. Detta skydd skulle bestå i att ju fler arter som finns, desto flera nischer är ockuperade. Det går dock att vända på resonemanget och säga att artrikedomen i en miljö är ett resultat av möjligheten för arter att etablera sig. Detta stämmer också väl överens med flera senare studier som funnit ett positivt samband mellan miljöers artrikedom och antalet etablerade främmande arter. Även min studie fann stöd för det senare påståendet. Jag fann att etablerade populationer av främmande vattenväxter var vanligare i att artrika sjöar än i artfattiga sjöar. Detta resultat kan förklaras med att mottagligheten för främmande arter är större i artrika miljöer är i artfattiga miljöer, och en trolig förklaring är att artrika miljöer har en större mängd olika livsmiljöer.

Den andra studien testade hur den Europeiska utbredningen av främmande arter kan tänkas förändras med den förväntade klimatförändringen. Ekologiska nischmodeller utvecklades för 13 främmande arter som redan idag är etablerade och orsakar problem i delar av Europa. Dessa modeller baserades på information om arternas nuvarande utbredningsmönster, nuvarande klimatförhållanden och förväntat framtida klimat. Resultaten visade att de främmande arter som idag orsakar problem i Centraleuropa troligtvis kan etablera sig och skapa problem även i Sverige i slutet av detta århundrade.

Övriga tre studier behandlade effekter och spridning av den främmande flytbladsväxten sjögull. Sjögull, som introducerades i Sverige i slutet av 1800-talet, finns idag i ett 30-tal svenska sjöar och vattendrag. Växten har ofta en snabb spridning och kan bilda mycket täta bestånd, vilka kan vara ett hinder för bad, fiske och sjöfart. De täta bestånden utgör troligen också en stor påverkan på ekosystemet, främst genom förändrat ljusklimat. Två av avhandlingens studier undersökte vilken påverkan sjögull har på andra, mer bottenlevande, vattenväxter. Båda dessa studier fann att sjögull troligen orsakar förändringar av det naturliga växtsamhället redan vid låga eller måttliga tätheter.

I och med de besvär som sjögull för med sig för människan utförs på flera håll i landet bekämpning av arten. Denna bekämpning består oftast i slåtter, det vill säga avklippning några decimeter under vattenytan. Eftersom de avklippta växtdelarna inte tas omhand, finns risken att de transporteras med vattenströmmar till nya områden där de kan etablera nya bestånd. Det har dock tidigare varit ytterst osäkert om spridningen av sjögull berott på att växtdelar lossnat, transporterats

och slagit rot, eller om spridningen skett med frön. För att kvantifiera betydelsen av olika spridningssätt hos sjögull gjordes därför en genetisk studie. Resultaten av den genetiska studien visade att fröspridning bara förekom i ett vattensystem, och där endast i begränsad omfattning. Betydligt vanligare var den vegetativa förökningen. Den stora betydelsen av detta förökningssätt medför att de bekämpningsmetoder som idag används accelererar spridningen av arten.

References

Albright, T., Moorhouse, T. & McNabb, J. 2004. The rise and fall of water hyacinth in Lake Victoria and the Kagera River Basin, 1989-2001. *Journal of Aquatic Plant Management 42*, 73-84.

Alpert, P., Bone, E. & Holzapfel, C. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology Evolution and Systematics 3*, 52-66.

Baker, H.G. 1974. The evolution of weeds. *Annual Review of Ecology and Systematics 5*, 1-24.

Baker, R.H.A., Sansford, C.E., Jarvis, C.H., Cannon, R.J.C., MacLeod, A. & Walters, K.F.A. 2000. The role of climatic mapping in predicting the potential geographical distribution of non-indigenous pests under current and future climates. *Agriculture Ecosystems & Environment 82*, 57-71.

Barrett, S.C.H. 1992. Genetics of weed invasions. In: *Applied population biology*. Edited by S.K. Jain & L.W. Botsford. Kluwer Academic Publishers. Dordrecht. pp. 91-119.

Barrett, S.C.H. & Husband, B.C. 1989. The genetics of plant migration and colonization. In: *Plant population genetics, breeding, and genetic resources*. Edited by H.D. Brown, M.T. Clegg, A.L. Kahler & B.S. Weir. Sinauer. Sunderland. pp. 254-277.

Blossey, B. & Notzöld, R. 1995. Evolution of increased competitive ability in invasive nonindigenous plants – a hypothesis. *Journal of Ecology 83*, 887-889.

Blumenthal, D. 2005. Interrelated causes of plant invasion. *Science 310*, 243-244.

Blumenthal, D.M. 2006. Interactions between resource availability and enemy release in plant invasion. *Ecology Letters 9*, 887-895.

Boylen, C.W., Eichler, L.W. & Madsen, J.D. 1999. Loss of native aquatic plant species in a community dominated by Eurasian watermilfoil. *Hydrobiologia 415*, 207-211.

Brock, T.C.M., Arts, G.H.P., Goossen, I.L.M. & Rutenfrans, A.H.M. 1983. Structure and annual biomass production of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). *Aquatic Botany 17*, 167-188.

Callaway, R.M. & Maron, J.L. 2006. What have exotic plant invasions taught us over the past 20 years? *Trends in Ecology and Evolution 21*, 369-374.

Cook, C.D.K. 1985. Range extension of aquatic vascular plant species. *Journal of Aquatic Plant Management 23*, 1-6.

Cook, C.D.K. 1990a. Origin, autecology, and spread of some of the world's most troublesome aquatic weeds. In: *Aquatic weeds*. Edited by A.H. Pieterse & K.J. Murphy. Oxford University Press. Oxford. pp. 31-38.

Cook, C.D.K. 1990b. Seed dispersal of *Nymphoides peltata* (S.G. Gmelin) O. Knutze (Menyanthaceae). *Aquatic Botany 37*, 325-340.

Davies, K.F., Chesson, P., Harrison, S., Inouye, B.D., Melbourne, B.A. & Rice, K.J. 2005. Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology 86*, 1602-1610.

Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature 391*, 783 - 786.

Davis, M.A., Grime, J.P. & Thompson, K. 2000. Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology 88*, 528-534.

Davis, M.A., Thompson, K. & Grime, J.P. 2005. Invasibility: the local mechanism driving community assembly and species diversity. *Ecography 28*, 696-704.

di Castri, F. 1990. On invading species and invaded ecosystems: the interplay of historical chance and biological necessity. In: *Biological invasions in Europe and the Mediterranean basin*. Edited by F. di Castri, A.J. Hansen & M. Debussche. Kluwer Academic Publishers. Dordrecht. pp. 3-16.

Diehl, S. & Kornijów, R. 1998. Influence of submerged macrophytes on trophic interactions among fish and macroinvertebrates. In: Jeppesen, E., Søndergaard, M.,

Søndergaard, M., Christoffersen, K. (Eds.), The structuring role of submerged macrophytes in lakes. *Ecological studies 131*, 24-46.
Elton, C.S. 1958. *The ecology of invasions by animals and plants*. Methuen. London. 181 pp.
Goodwin, B.J., McAllister, A.J. & Fahrig, L. 1999. Predicting invasiveness of plant species based on biological information. *Conservation Biology 13*, 422-426.
Grotkopp, E., Rejmanek, M. & Rost, T.L. 2002. Toward a causal explanation of plant invasiveness: Seedling growth and life-history strategies of 29 pine (*Pinus*) species. *American Naturalist 159*, 396-419.
Guisan, A. & Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters 8*, 993-1009.
Guppy, H. 1897. On the postponement of the germination of the seeds of aquatic plants. *Proceedings of the Royal physical society of Edinburgh 13*, 344-359.
Hannah, L., Midgley, G.F. & Millar, D. 2002. Climate change-integrated conservation strategies. *Global Ecology and Biogeography 11*, 485-495.
Hastings, A., Cuddington, K., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A., Harrison, S., Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B.A., Moore, K., Taylor, C. & Thomson, D. 2005. The spatial spread of invasions: new developments in theory and evidence. *Ecology Letters 8*, 91-101.
Heger, T. 2001. A model for interpreting the process of invasion: Crucial situations favouring special characteristics of invasive species. In: *Plant invasions: Species ecology and ecosystem management*. Edited by G. Brundu, J. Brock, L. Camarda, L. Child & M. Wade. Backhuys Publishers. Leiden. pp. 3-10.
Heger, T. & Trepl, L. 2003. Predicting biological invasions. *Biological Invasions 5*, 313-321.
Herben, T., Mandak, B., Bimova, K. & Munzbergova, Z. 2004. Invasibility and species richness of a community: A neutral model and a survey of published data. *Ecology 85*, 3223-3233.
Hill, M.P. & Cilliers, C.J. 1999. *Azolla filiculoides* Lamarck (Pteridophyta : Azollaceae), its status in South Africa and control. *Hydrobiologia 415*, 203-206.
Holm, L.G., Plucknett, D.L., Pancho, J.V. & Herberger, J.P. 1977. *The world's worst weed: Distribution and biology*. University Press of Hawaii. Honolulu. 609 pp.
Huntley, B. 1991. How plants respond to climate change - Migration rates, individualism and the consequences for plant-communities. *Annals of Botany 67*, 15-22.
Johnson, L.E., Ricciardi, A. & Carlton, J.T. 2001. Overland dispersal of aquatic invasive species: A risk assessment of transient recreational boating. *Ecological Applications 11*, 1789-1799.
Johnstone, I.M., Coffey, B.T. & Howard-Williams, C. 1985. The role of recreational boat traffic in interlake dispersal of macrophytes: A New Zealand case study. *Journal of Environmental Management 20*, 263-279.
Jones, J.I., Li, W. & Maberly, S.C. 2003. Area, altitude and aquatic plant diversity. *Ecography 26*, 411-420.
Keane, R.M. & Crawley, M.J. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution 17*, 164-170.
Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D. & Reich, P. 2002. Biodiversity as a barrier to ecological invasion. *Nature 417*, 636-638.
King, S.A. & Buckney, R.T.G. 2000. Urbanization and exotic plants in northern Sydney streams. *Austral Ecology 25*, 455-461.
Kolar, C.S. & Lodge, D.M. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution 16*, 199-204.
Landis, W.G. 2004. Ecological risk assessment conceptual model formulation for nonindigenous species. *Risk Analysis 24*, 847-858.
Larson, D. & Willén, E. 2006. Främmande och invasionsbenägna vattenväxter i Sverige (in Swedish, with English abstract). *Svensk Botanisk Tidskrift 100*, 5-15.
Lockwood, J.L., Cassey, P. & Blackburn, T. 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution 20*, 223-228.

Lodge, D.M. 1993. Biological invasions: Lessons for ecology. *Trends in Ecology and Evolution 8*, 133-137.
Lonsdale, W.M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology 80*, 1522-1536.
MacArthur, R. 1972. Species packing and competitive equilibrium for many species. *Theoretical population biology 1*, 1-11.
Mack, R.N. 1996. Predicting the identity and fate of plant invaders: Emergent and emerging approaches. *Biological Conservation 78*, 107-121.
Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications 10*, 689-710.
Maki, K. & Galatowitsch, S. 2004. Movement of invasive aquatic plants into Minnesota (USA) through horticultural trade. *Biological Conservation 118*, 389-396.
McCarthy, M.A. 1997. The Allee effect, finding mates and theoretical models. *Ecological Modelling 103*, 99-102.
McCreary, N.J. 1991. Competition as a mechanism of submersed macrophyte community structure. *Aquatic Botany 41*, 177-193.
McKinney, M.L. & Lockwood, J.L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution 14*, 450-453.
Mitchell, C.E. & Power, A.G. 2003. Release of invasive plants from fungal and viral pathogens. *Nature 421*, 625-627.
Moreira, I., Ferreira, T., Monteiro, A., Catarino, L. & Vasconcelos, T. 1999. Aquatic weeds and their management in Portugal: insights and the international context. *Hydrobiologia 415*, 229-234.
Newman, J.R. & Dawson, F.H. 1999. Ecology, distribution and chemical control of *Hydrocotyle ranunculoides* in the UK. *Hydrobiologia 415*, 295-298.
Nichols, S.A. 1991. The Interaction between biology and the management of aquatic macrophytes. *Aquatic Botany 41*, 225-252.
Nyberg, C.D. & Wallentinus, I. 2005. Can species traits be used to predict marine macroalgal introductions? *Biological Invasions 7*, 265-279.
Olden, J.D., Poff, N.L., Douglas, M.R., Douglas, M.E. & Fausch, K.D. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution 19*, 18-24.
Ornduff, R. 1966. The origin of dioecism from heterostyly in *Nymphoides* (Menyanthaceae). *Evolution 20*, 309-314.
Ortega, Y.K. & Pearson, D.E. 2005. Weak vs. strong invaders of natural plant communities: Assessing invasibility and impact. *Ecological Applications 15*, 651-661.
Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Holle, B.V., Moyle, P.B., Byers, J.E. & Goldwasser, L. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions 1*, 3-19.
Pearson, R.G. & Dawson, T.P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography 12*, 361-371.
Peterson, A., Papes, M. & Kluza, D. 2003. Predicting the potential invasive distribution of four alien plant species in North America. *Weed Science 51*, 863-868.
Phillips, S.J., Anderson, R.P. & Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling 190*, 231-259.
Pimentel, D., Lach, L., Zuniga, R. & Morrison, D. 2000. Environmental and economic costs of nonindigenous species in the United States. *Bioscience 50*, 53-64.
Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T. & Tsomondo, T. 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture Ecosystems & Environment 84*, 1-20.
Prinzing, A., Durka, W., Klotz, S. & Brandl, R. 2002. Which species become aliens? *Evolutionary Ecology Research 4*, 385-405.

Rejmanek, M. 2000. Invasive plants: approaches and predictions. *Austral Ecology 25*, 497-506.
Rhymer, J.M. & Simberloff, D. 1996. Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics 27*, 83-109.
Richardson, D.M. & Pyšek, P. 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography 30*, 409-431.
Richardson, D.M., Pyšek, P., Rejmanek, M., Barbour, M.G., Panetta, F.D. & West, C.J. 2000. Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions 6*, 93-107.
Rørslett, B. 1991. Pricipal determinants of aquatic macrophyte richness in northern European lakes. *Aquatic Botany 39*, 173-193.
Rosenzweig, M.L. 2001. The four questions: What does the introduction of exotic species do to diversity? *Evolutionary Ecology Research 3*, 361-367.
Roy, J. 1990. In search of the characteristics of plant invaders. In: *Biological invasions in Europe and the Mediterranean basin*. Edited by F. di Castri, A.J. Hansen & M. Debussche. Kluwer Academic Publishers. Dordrecht. pp. 335-352.
Santamaría, L. 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. *Acta Oecologica 23*, 137-154.
Simberloff, D. & Alexander, M. 1998. Assessing risks to ecological systems from biological introductions (excluding genetically modified organisms). In: *Handbook of environmental risk assessment and management*. Edited by P. Calow. Blackwell Science. Malden, Mass. pp. 147-176.
Skov, F. & Svenning, J.-C. 2004. Potential impact of climatic change on the distribution of forest herbs in Europe. *Ecography 27*, 366-380.
Smits, A.J.M., van Avesaath, P.H. & van der Velde, G. 1990. Germination requirements and seed banks of some nymphaeid macrophytes: *Nymphaea alba* L., *Nuphar lutea* (L.) Sm. and *Nymphoides peltata* (Geml.) O. Kuntze. *Freshwater Biology 24*, 315-326.
Stastny, M., Schaffner, U. & Elle, E. 2005. Do vigour of introduced populations and escape from specialist herbivores contribute to invasiveness? *Journal of Ecology 93*, 27-37.
Stewart-Oaten, A., Murdoch, W.W. & Parker, K.R. 1986. Environmental impact assessment - "pseudoreplication" in time? *Ecology 67*, 929-940.
Stohlgren, T.J., Barnett, D.T. & Kartesz, J.T. 2003. The rich get richer: patterns of plant invasions in the United States. *Frontiers in ecology 1*, 11-14.
Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs 69*, 25-46.
Stohlgren, T.J. & Schnase, J.L. 2006. Risk analysis for biological hazards: What we need to know about invasive species. *Risk Analysis 26*, 163-173.
Taylor, C.M. & Hastings, A. 2005. Allee effects in biological invasions. *Ecology Letters 8*, 895-908.
Thuiller, W., Richardson, D.M., Pyšek, P., Midgley, G.F., Hughes, G.O. & Rouget, M. 2005. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology 11*, 2234-2250.
Tilman, D. 1999. The ecological consequences of changes in biodiversity: A search for general principles. *Ecology 80*, 1455-1474.
Uesugi, R., Goka, K., Nishihiro, J. & Washitani, I. 2004. Allozyme polymorphism and conservation of the Lake Kasumigaura population of *Nymphoides peltata*. *Aquatic Botany 79*, 203-210.
Uesugi, R., Tani, N., Goka, K., Nishihiro, J., Tsumura, Y. & Washitani, I. 2005. Isolation and characterization of highly polymorphic microsatellites in the aquatic plant, *Nymphoides peltata* (Menyanthaceae). *Molecular Ecology Notes 5*, 343-345.
van der Velde, G., Giesen, T.G. & van der Heijden, L.A. 1979. Structure, biomass and seasonal changes in biomass of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae), a preliminary study. *Aquatic Botany 7*, 279-300.
van der Velde, G. & van der Heijden, L.A. 1981. The floral biology and seed production of *Nymphoides peltata* (GMEL.) O. Kuntze (Menyanthaceae). *Aquatic Botany 10*, 261-293.

Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Rejmanek, M. & Westbrooks, R. 1997. Introduced species: A significant components of human-caused global change. *New Zealand Journal of Ecology 21*, 1-16.

Vrijenhoek, R.C. 1990. Genetic diversity and the ecology of asexual populations. In: *Population biology: ecological and evolutionary viewpoints*. Edited by K. Wöhrmann & S.K. Jain. Springer-Verlag. Berlin. pp. 175-198.

Wallentinus, I. 2002. Introduced marine algae and vascular plants in European aquatic environments. In: *Invasive aquatic species of Europe. Distribution, impacts and management*. Edited by E. Leppäkoski, S. Gollasch & S. Olenin. Kluwer Academic Publishers. Dordrecht. pp. 27-52.

Wang, Y., Wang, Q.F., Guo, Y.H. & Barrett, S.C.H. 2005. Reproductive consequences of interactions between clonal growth and sexual reproduction in *Nymphoides peltata*: a distylous aquatic plant. *New Phytologist 165*, 329-335.

Wetzel, R.G. & Søndergaard, M. 1998. Role of submerged macrophytes for microbial community and dynamics of dissolved organic carbon in aquatic ecosystems. In: Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K. (Eds.), The structuring role of submerged macrophytes in lakes. *Ecological studies 131*, 133-148.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. 1998. Quantifying threats to imperiled species in the United States. *Bioscience 48*, 607-615.

Williamson, M. 1999. Invasions. *Ecography 22*, 5-12.

Williamson, M. 2006. Explaining and predicting the success of invading species at different stages of invasion. *Biological Invasions 8*, 1561-1568.

Williamson, M. & Fitter, A. 1996a. The characters of successful invaders. *Biological Conservation 78*, 163-170.

Williamson, M. & Fitter, A. 1996b. The varying success of invaders. *Ecology 77*, 1661-1666.

Acknowledgements – Tack

Tack till alla som har bidragit till denna avhandlings tillkomst.

Först av allt vill jag tacka mina handledare **Eva Willén** och **Ulf Grandin** för all den hjälp och kunskap jag fått av er under min tid som doktorand. Jag är även tacksam till alla andra vid Institutionen för Miljöanalys som hjälp mig under de gångna åren. Särskilt vill jag tacka **Jakob Nisell**, **Micke Östling**, **Hasse Eurell**, **Stellan Sjödahl** och **Tommy Jansson** som hjälpt mig allt från GIS till diverse praktiska göromål. Jag är dessutom tacksam till alla doktorander som utgjort ett mycket trevligt sällskap. Att vara doktorand vid SLU för med sig en rättighet till en 5 m^2 stor arbetsyta. Eftersom ingen vettig arkitekt ritar så pass små arbetsrum har jag under min tid som doktorand alltid delat rum med andra doktorander. Jag har dock varit lyckligt lottad och haft väldigt trevliga rumskamrater: **Jenny Bergfur**, **Neil Cory**, **Sonja Stendera** och **Ina Bloch**.

Alla i projektet AquAliens förtjänar ett stort tack. Det har varit ett stort nöje och en nyttig erfarenhet att arbeta i detta, ibland tungrodda, tvärvetenskaplig projekt. De möten vi haft har varit en stor källa till inspiration, men också inneburit många trevliga stunder och mycket god mat. Resan till Kanada innebar många oförglömliga minnen, bland annat av diverse stora valar. Ett särskilt tack vill jag rikta till **Malin Werner** som, förutom att arrangera mycket av det praktiska inom projektet, har gett mig många uppmuntrande ord när de behövts som mest. Ett särskilt tack förtjänar även **Cecilia Nyberg** och **Ullrika Sahlin** som fått arbeta dag och natt för att hinna klart med vårt gemensamma manuskript till denna avhandlings tryck. Projektet AquAliens hade aldrig blivit till om det inte vore för finansiering från Naturvårdsverket. **Melanie Josefsson** vid Naturvårdsverket var även en stor källa till inspiration och gav mig en bra introduktion i ämnet.

Jag vill även tacka alla som på andra sätt bidragit till avhandlingens tillkomst. Jag har i mitt fältarbete haft stor hjälp av **Therese Carlsson**, **Jonny Darabant**, **Malin Eriksson**, **Simon Hallstan** och **Staffan Åkerblom**. Därutöver har **Inger Wallentinus** och **Eva Willén** samlat in prov från avlägsna delar av Sverige. **Inger Jonasson** och **Jenny Jonsson** vid Rudbecklaboratoriet gjorde ett strålande arbete med de genetiska analyserna av sjögull och tog sig tid att diskutera resultaten med mig. Att skriva om främmande arter på ett främmande språk är inte alltid det lättaste. Jag vill därför även tacka alla som hjälpt till och kommenterat det jag skrivit, inte minst **Steve Scott Robson** och **Therese Carlsson**.